PLATE TECTONICS AND PROBLEMS OF ANGIOSPERM HISTORY

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Summary. — This review of current ideas regarding the influence of plate tectonics on angiosperm history leads to the following conclusions.

1. The primary angiosperm distribution patterns (tropical; tropical and extratropical; tropical and boreal; tropical and austral), were established by the Cretaceous when 3 major land areas, Laurasia, West Gondwana and East Gondwana were in proximity. Subsequent changes in distribution and evolution reflect the breakup of these lands by oceanfloor spreading.

2. Present discontinuous patterns across the tropics resulted from the isolation of taxa by ocean-floor spreading, and the elimination of some in local regions (e.g. *Nypa* in America).

Discontinuities between the Fuegan and Tasman regions developed after Eocene time as Antarctica was rafted into polar latitudes, and as increasing cold and winter darkness eliminated taxa there that earlier had linked all austral temperate lands.

The temperate forests of Holarctica were isolated by spreading cold and drought during Neogene time, brought on in large measure by the nortward movement of land masses, continental rotation and closing the arctic basin, and elevation of major cordileras.

Links between the sclerophyllous vegetation of California and the Mediterranean region via the southwestern United States, northern Mexico, the Appalachians, Canary Islands, and islands now subsea, are Paleogene chiefly, but some may be late Cretaceous.

3. Diverse factors account for changes in diversity of the surviving relict forests of the widespread Tertiary Geofloras. The New Zealand rainforest is richer than that of Chile because the former was rafted to a mild equable climate, was enriched by immigrants from the north via volcanic archipelagos and now-sunken sialic lands (Lord Howe Rise, Norfolk Ridge, etc.), and was removed from the cold and drought that restricted the area of the Chilean forest, eliminated many taxa there, and prevented its further enrichment from the north.

The endemic flora of the Australian dry region is much richer than that of India even though the latter was isolated longer. Australia was isolated following the Eocene and received few immigrants as it entered the dry tropics. By contrast, India was well forested into the Miocene when it joined the Asian plate. Aridity then increased, equability was lowered, and its western half was invaded by a semiarid to arid flora that had already evolved over southwestern Asia.

Fusion of Asian and Australian plates resulted in increased diversity throughout the region from southeast Asia to Australasia, not only over the lowlands but in temperate montane zones as well, and especially in the east—in New Guinea and bordering regions.

Complex plate motions during the later Cenozoic resulted in volcanism that built a bridge between North and South America for the first time since the pre-Cretaceous. This resulted in increased diversity over Mesoamerica, notably south of Mexico where austral temperate taxa as well as otherwise typically South American tropical families now occur. Relatively few North American temperate alliances appear to have penetrated southward (e.g. *Alnus*, *Quercus*).

During the Cenozoic Laurasia moved north and rotated to close the arctic basin, bringing colder and drier climates to continental areas. The mixed mesophytic forest of central China, shielded by mountains from

outbreaks of cold Siberian air masses, has preserved many Tertiary relicts and is the richest surviving forest of the Arcto-Tertiary Geoflora. The related forest in Japan has few relicts and is less diverse because it was more affected by cold during the Cenozoic. The lower diversity of the Appalachian forests reflects the vicissitudes of nearby glacial climates that eliminated many broadleafed evergreens and deciduous hardwoods that were there in the Tertiary. The deciduous forests of southwestern Eurasia show decreased diversity in response to lowered equability from the Black Sea region (Caucasus ; northern Turkey) to the lower Elbruz Mountains bordering the Caspian.

Plate tectonics provides insight into many problems of biogeography. Equally important, it also clarifies the guiding role that environment has had in evolution by providing a better basis for understanding the physical factors that have affected changes in diversity and controlled episodes of extinction and replacement. Prior to outlining some examples of these relations, as illustrated by angiosperms during Cretaceous and later times, the nature of plate tectonic theory is summarized first.

PLATE TECTONICS

The earth's crust is composed of a small number of rigid plates that are all moving with respect to one another, some at rates as high as 10 cm per year. Authorities recognize 6 major plates today, and some have also identified several subplates as well ; in Mesozoic time plates were less numerous than at present. Plates are from 50-100 km thick, they include both ocean basins and continents, and they are generally aseismic except at their boundaries where the moving plates jostle one another and result intense earthquake activity and volcanism.

Different types of movement occur at plate boundaries. First, as major rifting commences, lavas well up and solidify. Since this new crust formed by the outpouring basaltic lavas is added to the plate on each side of the rift, they move apart by lateral growth. As a result, continents, older sea floor, and oceanic islands are rafted to new positions. Second, moving plates are thrust back into the mantle along subduction zones at the site of ocean trenches (e.g. Chilean trench, Tonga-Kermadec trench) which usually are marked by island arcs typified by active volcanos (Kurile Is., East Indies). If a moving plate carries a continent to a subduction zone it may meet another continent and be thrust under it (India-Asia), elevating major mountain systems. Third, two plates may slide past one another without major plate modification, with the zone of movement being marked by a major transform fault (Alpine fault, New Zealand).

The sequence may start with the development of a great rupture within a continent, as in the present rift valleys of Africa, or between Africa-South America in the early Cretaceous along a line we now recognize as the mid-Atlantic Ridge. Since new ocean floor is continually formed at the rupture which develops into a mid-ocean rise, it follows that the present ocean floor is not very old; nearly half of it is of Tertiary age. As the lavas well up they come under the influence of the earth's magnetic field which reverses periodically. The solidified lavas retain a record of the magnetism which gives a distinct pattern of magnetic anomalies that can be recorded and identified. Inasmuch as their ages are determinable by both radiometric data and microfossil evidence, movement of the plates can be charted by identifying and mapping the dated anomalies. For older rocks, lavas on the continents are used to determine magnetic polar positions. By plotting the magnetic poles for progressively older rocks, a " wander curve " can be reconstructed that shows approximately the changing latitude of the continents.

The role of plate tectonics in biogeography and evolution is readily understandable. If newly-formed plates move apart, taxa with formerly continuous distributions become disrupted, as when tropical Africa and South America finally separated in the late Cretaceous (Turonian, 85-90 m.y.). Since isolation frequently results in the development of new taxa, formerly connected lands will share related species, genera, tribes or families, depending on the taxon, rate of evolution, and time involved. If continents are rafted across many degrees of latitude, they move into new climatic belts that provide new opportunities for some, but may result in the extinction of others, as in the case of India moving across the inner tropics and into the northern "horse latitudes" during the Paleogene. When two plates merge, taxa previously separated will intermingle, as when Australia moved north to meet the Asian plate, creating a zone of mixing along the newly-established Wallace's line during the Miocene, and increasing diversity of taxa there. By contrast, if a plate is broken into smaller ones that are rafted to new positions, new taxa may evolve in isolation, and the trend to more equable marine climate may favor the persistence of relicts, as in Australasia during the Tertiary.

Plate tectonics obviously provides a reliable basis for understanding events that have had a major role in biogeography and evolution. It is already clear that hypotheses that have visualized the survival of progressive waves of holarctic groups in the extremities of austral lands; or radiation of most vertebrate groups from the Old World tropics; or an "Assam to Fiji" heartland for the origin of angiosperms, are untenable. As demonstrated earlier by Brundin (1965) in his superb analysis of the evolutionary relations of fresh-water midges (Chironomidae), and discussed recently by Keast (1971) and by Fooden (1972), the history of global biota must be related to the successive stages of plate fragmentation or fusion. Unfortunately, reconstructions of the positions of the continents by earth scientists do not always agree. This is chiefly because the available data in some areas (e.g. Indian Ocean) are still meagre and interpolation is bound to result in disagreement and in some error. Although some widely-accepted reconstructions seem biologically impossible, these problems no doubt will be resolved within a few years as more evidence becomes available.

CRETACEOUS DISTRIBUTION PATTERNS

Many existing groups radiated during Cretaceous time, when the world was divided effectively into three major segments: Laurasia (Eurasia-North America), West Gondwana (Africa-South America) with direct access to western Eurasia via Africa, and East Gondwana (Australia-Antarctica) with direct access to West Gondwana via Antarctica-South America. A broad corridor did not exist for migration between North and South America during the Cretaceous, but migration to South America was possible via Laurasia-Africa. This Africa-South America (West Gondwana) link was finally severed in the early Turonian, leaving South America isolated from North America until the late Pliocene except for an archipelago that was a strong filter bridge. Migration between Australia-South America via Antarctica was possible into Eocene time. Numerous patterns of distribution correspond to one of the three areas, and to the times they were mutually accessible. These patterns have earlier been termed (Axelrod, 1960, Fig. 2) basically (a) tropical, (b) tropical-subtropical and north temperate, and (c) tropical-subtropical and austral temperate. Many typically northern and southern temperate alliances extend into warm temperate or subtropical regions today, and the record shows that they lived under similar climates during the later Cretaceous and Tertiary as well.

1. Among the alliances that had their primary radiation and diversification in Laurasia are Pinaceae (pine, fir, spruce, larch, hemlock, etc.), Taxodiaceae (redwood, swamp cypresss), Cupressaceae, Betulaceae, Corylaceae, Juglandaceae, Fagaceae, Salicaceae, Ranunculaceae, Berberidaceae, Cercidiphyllaceae, Trochodendronaceae, Aceraceae, Elaeganaceae, Nyssaceae, Hippocastanaceae, Staphylaceae, Magnoliaceae, Schizandraceae, Platanaceae, Cynocrambaceae, Calycanthaceae. Many of the woody dicots of these alliance are deciduous. This habit appears to have evolved in Laurasia under drought stress in warm temperate climates by the later Cretaceous, and to have preadapted them to live under the colder climates that developed later (Axelrod, 1966).

2. Some distributions suggest radiation from South America-Africa, notably in basically tropical families like Annonaceae, Bombacaceae, Burseraceae, Combretaceae, Connaraceae, Ebenaceae, Erythroxylaceae, Dilleniaceae, Flacourtiaceae, Lauraceae, Malpighiaceae, Hippocratiaceae, Meliaceae, Marantaceae, Melastomaceae, Musaceae, Myristicaceae, Olacaceae, Ochnaceae, Opilaceae, Palmae, Sapindaceae, Sterculiaceae, Zingiberaceae. During late Cretaceous to Paleogene time migration to tropical Asia was possible for plants adapted to subtropical to tropical climates, and they reached eastward into the tropical Pacific wherever volcanic archipelagos were present.

3. Some taxa occur on lands that have been connected with Antarctica, notably Winteraceae, Degneriaceae, Eupomatiaceae, Monimiaceae, Proteaceae, Chloranthaceae, Centrolpediaceae, Casuarinaceae, Epacridaceae, Restionaceae, Stackhousiaceae, Calyceriaceae, Stylidaceae, Pittosporaceae, Cunoniaceae. The strong representation of archaic angioperms in Australasia seems related to the increased insularity following Eocene time as the east margin of the Australasian plate was fragmented and displaced by oceanfloor spreading and transform faulting (Raven & Axelrod, 1972). Their survival is attributable to an equable marine climate more favorable for their preservation there than elsewhere, rather than to their origin in this region which was in southern temperate latitudes in Eocene time and earlier.

Apart from the basic patterns that distinguish these areas, each region has endemic families, some of which are autochthonous — notably those of the dry regions. However, many of those from moister areas have had wider distributions in the past, as Cercidiphyllaceae across Laurasia in the Tertiary (Brown, 1939), Nypaceae across tropical regions in the Cretaceous and Paleogene (Tralau, 1964) and Podocarpaceae (Couper, 1960) in the southern temperate latitudes, as well as northern.

ORIGINS OF DISCONTINUOUS DISTRIBUTIONS

Tropical Links.

Tropical South America and Africa were united into the early late Cretaceous, for the sedimentary sequences in each area show the encroachment of brackisb and then marine sedimentary environments across areas formely continental. Fossil pollen floras in the late Cretaceous deposits of tropical South America and Africa display great similarity, with some 34 of 39 taxa in common, which agrees with the near-identity of the ostracod and fresh-water fish faunas of the same region. Whereas these lands represented a single biogeographic province into the later Cretaceous, they are very different today.

The late Cretaceous (Turonian) and Tertiary separation of Africa and South America by continued ocean-floor spreading largely explains the present day occurrence of similar tropical families in each area (Axelrod, 1970; 1972a). Some of these alliances are preponderantly inner tropical, as Annonaceae, Bombacaceae, Burseraceae, Cochlospermaceae, Combretaceae, Connaraceae, Dilleniaceae, Hernandiaceae, Hippocrateaceae, Malpighiaceae, Marantaceae, Musaceae, Myristicaceae, Ochnaceae, Pandanaceae, Rhizophoraceae. A number of others that find optimum development and diversity within the tropics, and are represented in temperate regions by only a few small genera, also link these areas, as Acanthaceae, Anacardiaceae, Araceae, Bignoniaceae, Ebenaceae, Elaeocarpaceae, Flacourtiaceae, Gesneriaceae, Icacinaceae, Lauraceae, Leguminosae (Caesalpinoideae), Loganiaceae, Meliaceae, Monimiaceae, Moraceae, Palmeae, Passifloraceae, Rubiaceae, Sapotaceae, Simaroubaceae, Sterculiaceae. Other families link the African-American tropics, notably Canellaceae, Caricaceae, Humiriaceae, Hydnoraceae, Mayacaceae, Rapateaceae, Turneraceae, Velloziaceae, Vochysiaceae. Since all these alliances appear to have always been basically adapted to warm climates, they probably attained their distributions before the later Cretaceous, though stepping stones (volcanic islands, micro-continents like Azores plateau) were still sufficiently close to the retreating coasts into the Paleogene to enable some effective migration between tropical America-Africa.

The present distribution of these pantropic families is not the result of migration around high latitudes. It reflects older connections across the tropics and subtropics prior to the wide separation of land by oceanfloor spreading. This means that many woody angiosperm families were already in existence in the middle Cretaceous (Axelrod, 1970), though most modern genera had not yet appeared. Members of these (and other) pantropic families that link the American African with the Asian tropics extended along the shores of the Tethys during Cretaceous and early Tertiary times. They only reached eastward into the Pacific basin when lands in that area, chiefly volcanic, developed in response to the collision of plates, or to the appearance of volcanos that were built up over " hot spots " in the mantle and then rafted away on the moving Pacific plate.

Temperate Austral Links.

Temperate evergreen forests containing *Nothofagus* and its regular associates live today in the Tasman region (southeast Australia-Tasmania, New Zealand), in the temperate montane forests of New Guinea and New Caledonia, and in the Fuegan area (southern Chile, adjacent Argentina). Not only the forests, but related insects, fresh-water fish and midges, frogs, liverworts, earthworms, and other alliances link these regions. In addition, taxa of temperate requirements in southern Africa (e.g. Proteaceae, Cunoniaceae, Podocarpaceae, fresh-water midges, ratite birds) also indicate ancient links with both the Fuegan and Tasman regions.

The Proteaceae, best developed in Australia, have 3 distinct alliances in South Africa (*Dilobeia*; *Brabeium*; 13 of 19 genera of Proteeae). The closer affinity between the South American-Australasian then between the African-Australian proteads suggest a greater age for the latter (Johnson & Briggs, 1963), implying that the family is at least Albian-Cenomanian (110-100 m.y.). Analogous relations are seen in Cunoniaceae, and possibly Restionaceae which has diverse genera in Australia and one very unique assemblage of 10 genera in South Africa. Links are also provided by the families Chloranthaceae, Monimiaceae, Winteraceae. The genera *Hibbertia* (Dilleniaceae), and *Kerudarenia* and *Rulingia* (Sterculiaceae) are disjunct between Madagascar and Australasia, and presumably were earlier present in Africa.

The relations are understandable on the basis of the sequential breakup of Gondwanaland. As now understood, Africa (with India) separated from Antarctica-Australia in the early Cretaceous. Africa was joined to South America into the early Turonian (90 m.y.), providing a direct land connection via South America-Antarctica to Australia-New Zealand at that time. New Zealand separated from Antarctica-Australia in the late Cretaceous (80 m.y.), and Australia moved north from Antarctica in the Eocene (45 m.y.), the last time there was a direct connection between South America-Antarctica.

The relations of India are still uncertain in this scheme. Although many reconstruction (e.g. Dietz & Holden, 1970; Tarling, 1971; McElhinney, 1970; Heirtzler, 1970) show India as an island in the Indian Ocean during the Jurassic and Cretaceous, this does not meet paleontological evidence: India has late Cretaceous sauropod dinosaurs *(Laplatosaurus, Antarctosaurus, Titanosaurus)* that are recorded from other regions, notably Argentina, Europe, Africa and Australia. This suggest a later separation from India than has been proposed, and gives greater credence to a reconstruction such as that suggested by Veevers *et al.* (1971, Fig. 7). On this basis, the African links (proteads, etc.) with Australia may have been in the middle Cretaceous, whereas the closer affinity between the Australasian-Fuegan areas, as shown by the *Nothofagus* forests, may be late Cretaceous-Paleogene chiefly. This is a problem that only future evidence can settle.

Most reconstructions (e.g. Dietz & Holden, 1970; Heirtzler, 1971) place Antarctica in a polar position during Triassic and later times, which also poses a problem. Obviously, the Triassic *Lystrosaurus* fauna (Kitching, *et al.*, 1972) recorded from Lat. 85°S did not thrive under several months darkness and low temperature. There is also the problem of getting Cretaceous dinosaurs to Australia. It is unlikely that they could survive the low winter temperatures below Lat. 63°S, and foraging for food during the long winter night raises an additional problem. Nor is it probable that the Eocene evergreen forest (palm, Proteaceae, *Nothofagus*) reported from McMurdo South at Lat. 78°S lived at that high latitude. Antarctica more probably moved to its present position as the Antarctic-Indian Ocean rise was activated and the spreading sea floor rafted it to a polar position following the Eocene, as suggested by Cullen (1970) and also by Veevers *et al.* (1971).

Prior to this time, the Antarcto-Tertiary Geoflora, composed of *Nothofagus* and its associated broad-leafed evergreen dicots and conifers, formed a continuous southern forest, blanketing all the southern lands. Genera now confined to the Fuegan area have been recorded in the Tasman region, and some of the taxa with presently restricted ranges in the Tasman area were distributed much more widely there and across Antarctica into the Fuegan region (Axelrod, 1960, p. 270-273). As the austral land links were broken following the Eocene, forests now commenced to evolve in isolation, and with very different results in each area, as noted below.

Temperate Boreal Links.

Migration across Laurasia was direct and essentially uninterrupted during the Cretaceous. The late Cretaceous (Santonian-Campanian) sea that bisected central North America, and the late Cretaceous to Eocene (Maestrichtien-Lutetian) sea that ranged northward through the Uralian region did notgr eatly influence forest distribution. Later Cretaceous forests were generally similar across the north, but show regional climatic differences (Muller, 1970, Fig. 4), a relation maintained during the Tertiary (Axelrod, 1960, p. 269). Easy migration for mammals between eastern America and Eurasia continued into the early Eocene when the corridor was broken as ocean-floor spreading along the mid-Altantic Ridge extended the Atlantic into the arctic basin. However, the forests across the area were generally similar, representing mixed deciduous hardwood forests over the lowlands, and conifer-deciduous hardwood forests in the hills. Similarity continued into the Miocene, as shown by the fossil flora of Iceland that provides many links between western Europe and eastern North America; by the Miocene floras of Alaska that link that area with western Pacific States and the rich lloras of Japan-China ; and by the Miocene floras of eastern Europe-adjacent Russia that link that area with China-Japan.

These forest links across the temperate parts of Laurasia were broken in the Miocene by the spread of progressively drier and colder climates. This was ascribed initially by A. R. Wallace to general continental uplift, mountain building, and withdrawal of seaways from the continents during the Cenzoic. Northward movement of the American plate some 10° to 15° and closing the arctic basin by continental rotation is an additional crucial factor that brought progressively colder and more extreme climates to middle and high latitudes. As the interior regions of Eurasia and North America underwent progressive dessication, forests gradually retreated and patches of prairie in forest-border regions spread gradually to from extensive grasslands and steppes in which there was a great proliferation of new species and genera. As the northern forests retreated to somewhat lower latitudes in response to increased cold, taiga and then tundra plants spread out from earlier localized sites in mountainous areas, and gave rise to scores of new races, subspecies and species.

Mediterranean Links.

The sclerophyllous vegetation of California and the Mediterranean region share taxa that indicate ancient, trans-Atlantic connections (Axelrod, 1970, p. 309-310 ; 1973). Among the alliances in common are *Arbutus*, *Cercis*, *Cupressus*, *Helianthemeum*, *Laurocerasus*, *Lavatera*, *Myrica*, *Pinus* (" closed-cone pines ") *Quercus*, *Rhus*, *Rhamnus*. The affinities between these regions were stronger in the past, because *Clethra*, *Ilex*, *Persea*, *Pistacia*, *Nectandra* and *Sapindus* were also common to each region during the middle and late Tertiary. Some of these survive in the Mediterranean region today, but disappeared from California during the Pliocene as summer rainfall decreased. However, they are represented in the southwestern United States and in Mexico there they contribute to sclerophyllous vegetation that survives under subhumid to semiarid climates with summer rainfall, conditions like those of the Tertiary under which it thrived.

At the present time these areas are linked by related vegetation in intermediate regions. The laurel forest of the Canary Islands has number of plants that are similar to those that inhabited the nearby mainland during the Miocene (Depape, 1928). Furthermore, a good number of them occur also in the Azores, as *Erica*, *Hedrea*, *Ilex*, *Juniperus*, *Lavatera*, *Myrsine*, *Notolaea*, *Persea*, *Prunus*, *Rhamnus*, *Rhus*, as well as in the Mediterranean region. Another link is provided by *Pinus pungens* on the dry rocky slopes of the Alleghanies (e.g. North Carolina, alt. 3,500-4000 ft.), which is related to the " closed cone " pines of Mexico, California, and the Mediterranean. And others are seen in the sclerophyllous vegetation (oak woodland. chaparral) of northeastern Mexico that has species related to those in California and the Mediterranean area (*Pistacia*, *Persea*, *Myrica*, *Pinus*, etc.).

Further, distributional data summarized by Meusel (1971) and discussed in detail by Meusel and Jager (1971) show that numerous woody plants—many of them sclerophyllous — of the present Mediterranean flora also range discontinuously eastward into the Himalayas. Among these are species of *Berberis*, *Buxus*, *Cedrus*, *Cotinus*, *Cotoneaster*, *Daphne*, *Hedera*, *Ilex*, *Juniperus*, *Nerium*, *Punica*, *Quercus* (*ilex* group), *Pinus* (*canariensis-roxburghii*), *Zizyphus* and others. To judge from the fossil record, they appear to be part of an ancient Tethyan-border sclerophyllous flora that stretched more or less continuously across the drier southern latitudes of Eurasia and North America in the late Cretaceous and early Tertiary.

Interpretation of the relations is aided by the realization that the sclerophyllous vegetation in each region is bordered by derivative members of the Arcto-Tertiary Geoflora that ranged widely across the temperate parts of Holarctica during the Tertiary and late Cretaceous. These are represented by related species now in temperate Europe, eastern Asia, western America and eastern North America, including conifers (*Abies*, *Picea*, *Pinus*) as well as angiosperms (*Acer*, *Aesculus*, *Alnus*, *Betula*, *Cercis*, *Clematis*, *Cornus*, *Crataegus*, *Platanus*, *Populus*, *Quercus*, *Rhamnus*, *Rosa*, *Salix*, *Smilax*, *Sumac*, *Viburnum*, *Vitis*). In California and the Mediterranean — Himalayan region they occur chiefly in the mountains where there is higher rainfall and where temperatures are lower in summer. They usually descend into the lowlands on streambanks in cool, moist sites in areas otherwise characterized by sclerophyllous vegetation. They occur also in the mountains of Mexico where they border the sclerophyllous vegetation as well. Furthermore, in summer rainfall areas today, there are numerous other genera — *Carpinus*, *Diospyros*, *Fagus*, *Gleditsia*, *Liquidambar*, *Nyssa*, *Robinia*, that occurred with the above mentioned alliances during the Tertiary.

In areas of summer rainfall south of the desert regions, as in Mexico, Africa, and India-Pakistan, sclerophyllous vegetation is adjacent to thorn scrub, savanna and evergreen forest. The general similarities between the floras of the rainforest and bordering savanna vegetation of America and Africa have been noted by others (e.g. Engler, 1905; Hutchinson, 1946; Camp, 1947; Boughey, 1957), Aubreville, 1969). There are also links between the evergreen montane rainforests of Africa and Americа (Boughey, 1965; Miranda, 1959), including *Aralia*, *Dalbergia*, *Diospyros*, *Eugenia*, *Ficus*, *Ilex*, *Myrica*, *Podocarpus*, *Rhamnus*, *Sapindus*, *Sterculia*, *Zizyphus* and others. Apart from the genera common to the mesophytic evergreen lowland and montane rainforests and savana that range from the inner to outer tropics, plants adapted to open drier regions also provide links across the tropics. These are in *Acacia*, *Bursera*, *Cardiospermum*, *Celtis*, *Commiphora*, *Lycium*, *Maytenus*, *Prosopis*, and others (see Engler, 1914).

Additional links are provided by the similarities between the Cretaceous floras of the eastern United States and those of southern Europe (southern France, Spain), as noted by Berry (1916), and more recently by Depape (1959; 1963) and Teixiera (1952). The links between the Cretaceous temperate rainforests of these areas are provided by similar ferns, conifers and angiosperms, notably *Bauhinia*, *Laurus*, *Liriodendron*, *Magnolia*, *Palmae*, *Platanus*, *Myrtaceae*, *Quercus*, and others. Not only are the genera similar, some species appear to be indistinguishable. The Raritan flora (Hollick, 1895, pl. 21), and possibly the Dakota as well, have leaves very similar to those of *Arbutus canariensis*, which is now restricted to the Canary and Madeira islands. In addition, recent palynological evidence (Wolfe & Pakiser, 1971) indicates that the floras of eastern United States (Atlantic coastal area) and western Europe were rather similar to the Cenomanian, and that the important differences had developed later in the period.

In sum, there are recurring links between tropical rainforest, montane rainforest, savanna, thorn scrub vegetation, as well as the deciduous hardwood and conifer hardwood forests in more temperate climates on opposite sides of the Atlantic today. Since they displayed greater similarities in the past, it seems probable that the ties between the small, now restricted areas of mediterranean climate may have a similar explanation because the links between them were also more numerous in the past than they are today. These must reflect earlier land connections across the Atlantic (Dietz & Holden, 1970; Tarling, 1971; Dietz & Sproll, 1970) that have since been removed by seafloor spreading and by subduction. In the late Cretaceous and early Tertiary the Atlantic basin was shallow, its northern sector was just commencing to open, and was not very wide at middle latitudes. This is where the Canary plate (Dietz & Sproll, 1970), comprising a sialic fragment associated with younger volcanic rocks (composite island, sensu Axelrod, 1960, p. 283), is situated. Migration was no doubt possible into Paleocene or Eocene time because islands were present along the Mid-Atlantic ridge; they have since been transported laterally to subsea positions by spreading on the mid-ocean rise. As for the middle latitudes, migration would have been possible entirely within a region where, theoretically, warm and dry climate would be present. This agrees with the thick evaporite sequences that are recorded in Florida, the Gulf States and northern Mexico, as well as in southern Europe and north Africa at this time. It seems highly likely that from late Cretaceous into the Paleogene, migration across lower-middle latitudes via subhumid to semiarid corridors was possible for sclerophyllous plants, notably those of oak-laurel forest and oak woodland and sclerophyllous scrub vegetation. In brief, the floras of the present northern mediterranean regions which became adapted to the summer-dry mediterranean climate only since the Tertiary (Axelrod, 1973), include ancient alliances of dry regions that were derived ultimately from laurophyllous forests (see Meusel, 1971, p. 65; Axelrod, 1973) supplemented by newer taxa that have evolved more recently in isolation.

ISOLATION AND EVOLUTION

Tropical Forests.

As a plate is sundered and its parts are rafted away, new taxa commence to evolve in isolation. In time, new species and then genera appear that form members of a well-knit tribe or subfamily that may be restricted to one continental area. In many cases, a tribe common to two or more continental regions (e.g. tropical America, Africa) is represented by different genera in each area. For example, Table 1 lists the tribes of 3 typical pantropical families, and the number of genera in each tropical region. The presumption is that many of the genera evolved in isolation, though some had wider occurrences in the past and were restricted to their present areas, as the fossil record clearly shows. The distinctness of these taxa, often at tribal level, indicates that they have been long isolated and the families they represent must have considerable antiquity (late Cretaceous or older). The greater differences between them, as compared with taxa in temperate boreal or austral regions, is also consistent with their greater age, and agrees with current evidence regarding the ages of forest connections in those areas.

Table 1. — Distribution of genera of tribes of 3 pantropical families. Numbers in parenthesis indicate genera that occur in two or more regions.

	America	*Africa*	SE. Asia-*Australasia*
MORACEAE			
Moroideae			
Fatuocae	0	1 (2)	2 (2)
Moreae	1 (1)	2 (1)	7 (1)
Broussonetieae	2 (1)	1 (1)	4
Strebleae	0	1	5
Dorstenieae	(1)	3 (1)	1
Artocarpoideae			
Euartocarpea	8 (1)	1 (2)	1 (2)
Olmedieae	9	2 (1)	1 (1)
Brosimeae	2 (2)	4 (2)	1 (1)
Ficeae	(1)	(1)	1 (1)
Conocephaloideae	3	2	3
MALPIGHIACEAE			
Malpighieae	17	0	0
Tricomerieae	5	0	0
Gaudichaudieae	6	0	0
Hiraeeae	10	8	2
Banistericae	6 (2)	5 (3)	1 (1)

FLACOURTIACEAE

Berberidopsideae	1	5 (1)	2 (1)
Oncobeae	4 (1)	8 (1)	0
Scolopieae	1	7	2
Pangieae	1	1	11
Flacourtieae	6 (1)	4 (2)	5 (3)
Cascarieae	13 (1)	2 (1)	2 (1)
Banareae	2	2	0
Homalieae	1	6	0
Altzateae	1	0	0
Bembicieae	0	2 (Madag)	0

Temperate Forests.

Related forests that are widely separated in temperate regions commonly have different, though related species of the same genera. The case of the segregates in the discontinuous forests descended from the Arcto-Tertiary Geoflora is well documented (Li, 1962; Tralau, 1963). The differences between the modern species have arisen since the Miocene in large part, as judged from the Miocene forests of Alaska that have many species similar to those in the Miocene of Japan and the Pacific States; from the Miocene forests of Iceland that provide a link with those in western Europe and the present Appalachian region; and from the Miocene-Pliocene floras of eastern Europe-western Asia that have numerous links with those in eastern Asia. In most cases the differences between related species of pine, spruce, fir, oak, elm, beech, hornbeam, willow, poplar, etc. are minor. Species of the same tribe (or section) of a genus often occurred in all three areas during Oligocene and Miocene, but their present ranges are more restricted.

In the case of the Antarcto-Tertiary Geoflora, with its derivatives now confined chiefly to the Fuegan and Tasman regions, the species of some ancient genera in these regions are so different they could be considered separate genera (e.g. *Eucryphia*). In many instances, species of the austral evergreen forests show greater differences than do those in the discontinuous temperate deciduous hardwood and conifer hardwood forests of Holarctica. This is expectable since the austral connections were broken in the Eocene, as compared with the Miocene and later in the north: divergent evolution has proceeded farther in the south. Future detailed studies of both megafossil and microssil floras of these presently isolated areas will no doubt illuminate the history of these taxa more fully.

CHANGES IN DIVERSITY

New Zealand vs. Chile.

The temperate mixed evergreen dicot and conifer forests forming the Antarcto-Tertiary Geoflora were similar from New Zealand-Australia to Chile-Argentina *via* Antarctica. Genera now confined to one region had wider distributions in the past. *Nothofagus* occured on Antarctica and Kerguelen; species of the *N. brassii* group, now in New Guinea and New Caledonia, are represented in Australia-Tasmania-New Zealand and Argentina; *Araucaria* is recorded on Antarctica, Kerguelen and New Zealand; *Dacrydium*, now restricted to Tasmania, is known from Chile, Kerguelen, New Zealand and southern Australia; Proteaceae and Palmeae are recorded on Antarctica; and *Microcachrys*, now confined to Tasmania, was on Kerguelen, New Zealand and Australia.

As Godley (1960) noted, the temperate rainforest of New Zealand is much richer in taxa than that of southern Chile at the same latitude. 39 angiosperm families are common to both areas, 7 in Chile are not in New Zealand, and 24 families in New Zealand are not in southern Chile. These include Chloranthaceae, Corynocarpaceae, Icacinaceae, Lauraceae, Meliaceae, Moraceae, Myristicaceae, Palmeae, Pandanaceae, Passifloraceae, Piperaceae, Sapindaceae, Tiliaceae, all tropical-subtropical alliances.

Inasmuch as the fossil record shows that the forests were rather similar across the region into Oligo-Miocene time, the differences reflect their subsequent histories. Many alliances persisted in New Zealand because it was rafted to a more equable marine climate and was largely removed from the effects of severe cold or drought. Furthermore it was being enriched by immigrants from the north *via* new archipelagos (Solomons, New Hebrides), and also from the now largely submerged Norfolk Ridge and Lord Howe Rise which were then extensive land areas. Thus it is understandable that there is a rich representation of archaic plants in Australasia today (Raven & Axelrod, 1972), some of which (*Casuarina*, *Acompyle*, *Podocarpus* sect. Dacrycarpus) were earlier in Chile-Argentina. By contrast, the Chilean region did not shift in latitude, and the forest could not receive new immigrants. As drought spread down the west coast, the forests retreated southward to moister latitudes. With the late Tertiary uplift of the Andes, drier and colder climate spread over the Argentine plain, confining temperate rainforest that had dominated there into Miocene time to the moist slopes of the Andes. Glacial climate then spread along the Andine axis, and down onto the plains to the east and west, further decimating the remaining forest, and leaving only hardy relicts in the surviving impoverished community.

Australia vs. India.

As the Australian plate moved to lower latitudes following Eocene time, it entered the permanent high pressure belt of low precipitation at the south margin of the tropics. The temperate rainforest composed of southern beech, araucarias, podocarps, laurels, and other evergreen dicots that had covered much of the continent was restricted to moist, equable southeast Australia-Tasmania. During this movement, many taxa underwent great restrictions in range, and others must have become extinct. Some that were in the region survive now as relicts on the offshore lands of Australasia (New Caledonia, Fiji, Lord Howe I., Norfolk I.).

Rafting Australia into a new climatic belt provided new opportunities for evolution (Raven & Axelrod, 1972). As it moved into zone of warmer, drier climate, *Acacia*, *Eucalyptus*, *Grevillia*, *Melaleuca*, *Hakea*, *Eremophila* and others proliferated into scores of new species adapted to progressively drier, more continental climates. As drought continued to spread over the interior, new opportunities appeared for temperate austral families which evolved a wholly new flora composed of desert and desert-border alliances restricted to the drier parts of Australia. Some of these had earlier evolved scleropyllous representatives in areas of poor soil or in local arid sites provided by crystalline rock outcrops (Axelrod, 1972b).

By contrast, the origin of the arid flora of India was quite different. India probably separated from Africa, or from one of the sundered lands connected to it (e.g. Madagascar-Seychelles Plateau), during the Cretaceous-Paleocene transition. As noted above, earlier isolation of the subcontinent in the Indian Ocean, as depicted by Dietz and Holden (1970), Jardine & McKenzie (1972) and others, is improbable simply because large late Cretaceous sauropod dinosaurs (*Lapatosaurus*, *Antarctosaurus*, *Titanosaurus*) are recorded there (see Keast, 1971), as well as on other continents. Situated near Lat. 30°S in latest Cretaceous time, as judged from paleomagnetic evidence, India then supported southern temperate taxa (araucaria, proteads, casuarina, leptodactylid frogs) that are no longer on the subcontinent. Also present were genera of tropical to subtropical families including Musaceae, Zingiberaceae, Palmaceae, Nypaceae, Cyclanthaceae, Flacourtiaceae, Bombacaceae, Tiliaceae, Elaeocarpaceae, Simaroubaceae, Burseraceae, Meliaceae, Sapindaceae, Leguminosae, Combretaceae, Myrtaceae, Lauraceae, Myricaceae, and others (see Lakhanpal, 1970).

Although India was isolated somewhat longer than Australia, it has relatively few endemics because of its very different history (Axelrod, 1972c). As India commenced to move north during late Cretaceous-Paleocene time it was well blanketed with forest. As it moved across the inner tropical belt a number of the older austral temperate taxa probably were unable to adapt to the torrid thermal regime. Furthermore, they could not escape, because the region was low and mountains of sufficient altitude were not commonly present for their continued existence. Only *Hortonia*, an archaic angiosperm of monimiaceaous affinity that is the only member of its family and endemic to Ceylon, appears to be an austral angiosperm that survived on the Indian subcontinent. The tropical-subtropical alliances that survived then encountered rapidly expanding aridity as India entered the dry belt on the north margin of the tropics, as the Indian plate was welded to Asia, and as the general global trend to aridity progressed. Spreading aridity eliminated savanna forests in the west (Kutch, Rajasthan), and confined them to the central and eastern parts. The Neogene rainforest of the central region was restricted farther east (Assam-Malaya). Much of western and part of central India was invaded by a flora that had *already* evolved in response to dry climate which had appeared over southwest Asia by Eo-Oligocene time. Thus it is understandable that whereas many of the taxa in the tropical scrub and desert vegetation of India range far to the west (Iran-Arabia-Egypt), those in Australia are confined there because they developed and remained in isolation. It is apparent that the impoverishment of the Indian flora reflects its later history, in which floras of other regions (moist tropical southern Asia; dry southwest Asia) invaded the area as climates were altered and plants responded.

Increased diversity also resulted from the fusion of the Australian and Asian plates during the Miocene. This enabled taxa of austral subtropical regions to mingle with those of subtropical requirements, and those of austral temperate relations to penetrate into the cooler mountain climates (e.g. *Nothofagus*, *Podocarpus*, etc. in the mountains of New Guinea), with a few reaching eastward through the East Indies and adjacent islands to southeast Asia. The high diversity of taxa in this region thus results not wholly from evolution *in situ*, but from the addition of taxa by the rafting of a wholly new flora to lower, warmer latitudes.[1] The fragmentation of the east margin of the Australian plate by seafloor spreading and transform faulting following the Eocene has provided insular refuges for numerous warm temperate to mild temperate relicts in New Caledonia, New Zealand, Fiji and adjacent lands (Raven & Axelrod, 1972).

Increased diversity of the forests over Mesoamerica was also made possible by plate movements. The complex plate history in the region from the northern Andes into Mesoamerica is imperfectly known owing to a lack of geologic mapping and the absence of critical geophysical data. The general picture that emerges in one of complex plate movements in which the Cocos and Caribbean plates have played important roles between the Pacific and American plates. It now appears that gross relative motion of northern South America is counterclockwise with respect to the Pacific, Panama and Caribbean plate (Case, *et al.*, 1971). During the Cretaceous and most of the Tertiary there was a broad sea between North and South America. Island arcs were no doubt present and enabled some plant migration, but a corridor for movement was lacking into the late Tertiary. At this time complex plate movements resulted in the volcanism that built up the connection across Panama, linking North and South America. Numerous South American taxa moved north, reaching well into Mesoamerica. These included taxa from the lowland rainforest and savanna, as well as the paramo (Costa Rica). Relatively few northern temperate forest trees appear to have reached southward into the Andes (e.g. *Alnus*, *Quercus*), though numerous north temperate herbs were by now using the newly elevated volcanic highlands as way stations from northern North America to Fuegia.

Holarctic Temperate Regions.

The mixed deciduous hardwood forest that made up the conspicuous part of the Arcto-Tertiary Geoflora was widely distributed across temperate northern latitudes into Miocene time. Its later history reflects the effects of plate tectonics on climate during Neocene time, notably the increased altitude of land areas, the building up of major mountain systems, closing the arctic basin by continental rotation, and the movement of Antarctica to a polar position. These changes brought more extreme climates to areas previously characterized by ample rainfall and mild temperature. As a result, the mixed deciduous forests were eliminated entirely from some areas (western United States, western Mediterranean), or impoverished in others in greater (eastern Mediterranean-Transcaucasia)

1. These relations have been discussed at tedious length by Schuster (1972). Unfortunately, his unfamiliarity with the literature of plate tectonics has tended to leave many otherwise straightforward relations both obscured and confused.

or lesser degree (China, Japan). The important differences in diversity in areas where the derivative forests survive reflect the amount of summer rainfall and the equability of climate.

The richest living mixed deciduous-evergreen forest is in western Hupeh and adjacent Szechuan, a forest with numerous taxa and also one with many relicts of earlier times (e.g. *Ginkgo*, *Metasequoia*, *Cathaya*, *Keteleeria*, *Cercidiphyllum*, *Euptelea*, *Tetracentron*). Their persistance here reflects the mild winter climate at moderate altitudes (± 1.500 m) in a region that is shielded by mountains from the cold, Siberian air masses. In this region of ample summer rainfall frost is rare in winter and snow is virtually unknown : the forest must live under an equability of about *M* 60. Central Japan also has a rich mixed forest in the mountains, but it is not so diverse as that of central China. This is chiefly because the region was affected by the glacial climate, and numerous taxa that were there into the later Pliocene survive now only in central China. Today, equability in Japan is *M* 53-54 in the mildest sites, with ample rainfall through the year. By contrast, the mixed forests of the Appalachians are less diverse than those of Japan or China, evergreens are greatly reduced or absent, and the vegetation has co-dominants. The lower diversity of the forest is a result of the glacial ages because it could not escape by migration southward owing to a dry corridor between the Appalachians and the mountains of Mexico where a forest related to that of the Tertiary now survives. It lives under a mild winter climate with an equability rating of *M* 60-65, as compared with *M* 52-53 for the most equable parts of the mixed forest in the Appalachians today.

The largest relict Arcto-Tertiary forests in western Eurasia are in the Caucasus, the mountains of Turkey-Greece, and on the lower northern slopes of the Elburz Mountains.In these areas summer drought is absent (Causasus), or limited to 1 1/2 to 2 months and followed immediately by heavy rains. During the dry season clouds that build up from the adjacent Black and Caspian seas moderate temperatures in the mountains and reduce evaporation. As equability in these areas decreases, the diversity of the forests is lowered from *M* 55-57 on the lower slopes of the southern Caucasus, to *M* 54-55 in the southern Black Sea area, to *M* 52-54 in the *Parrotia* forest bordering the Caspian.

PLATE TECTONICS AND PROBLEMS OF ANGIOSPERM HISTORY

Addendum

More recent evidence (C. McA. Powell and P. J. Conaghan, " Plate tectonics and the Himalayas ", Earth and Planetary Sci. Letters 20 : 1-12, 1973) now indicates that the Himalayas have developed in two stages. The first involves convergence of the north-moving Indian landmass with the Tibetan region during the Late Cretaceous and Paleocene, with collision before the Middle Eocene. The second stage involves formation of a major crustal fracture within the Indian block during late Eocene and Oligocene, and underthrusting of the Indian subcontinent along this fracture from Miocene to Recent. Thus, the present elevated Himalayan chain is not a direct result of continent-continent collision as had earlier been supposed, but of uplift during underthrusting along a deep crustal fracture.

This revision of Indian structural history means more rapid movement of the Indian subcontinent northward during Late Cretaceous to Early Eocene time. This would have resulted in widespread extinction of austral, warm temperate taxa, as well as those of subtropical to tropical requirements, as the Indian land mass moved across the hot inner tropics and then into the dry belt in the Northern Hemisphere. This new evidence clearly lends greater credence to the general conclusions adduced above with respect to the origin of the Indian flora, and especially the factors that account for its impoverishment.

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DISCUSSION

Intervention du Professeur R. F. Laurent

Question

When, according latest estimates, did India begin its northward travel, and when did it reach Asia ?

Réponse

Only a tentative answer can now be given because so much additional work remains to be done in terms of unravelling the complex history of the Indian Ocean basin. The most recent evidence available to me is that synthetized by Sclater and Mckenzie (1972). It indicates northward movement commenced very late in the Cretaceous, with India ploughing into Asia near the Oligo-Miocène transition, at which time the Himalaya commenced to rise.